FEEDING-SITE SELECTION AND FORAGING STRATEGIES OF AMERICAN WOODCOCK

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Abstract.—Live-trapped, adult American Woodcock (*Scolopax minor*) were tested in a series of laboratory experiments designed to evaluate the role of soil as a proximal cue for selecting feeding sites and to investigate foraging strategies for capturing earthworms (Lumbricidae). Foraging trials were conducted in a circular arena and showed that color, which tends to be correlated with the soil types and moisture regimes preferred by earthworms, was an important proximal cue for selecting feeding sites. Woodcock captured earthworms most efficiently in areas of relatively high prey density, because they used a nonrandom search pattern following an initial capture. *Received 17 November 1981, resubmitted 4 August 1982, accepted 8 February 1983.*

Woodcock (*Scolopax minor*) obtain most of their food by probing subterraneanly (Sheldon 1971, Liscinsky 1972). This method of foraging does not permit birds to assess prey abundance visually at a site. Thus, woodcock are likely to expend time and energy searching in unprofitable areas unless they use some proximal cue to the habitat to improve their chance of selecting profitable sites. Food-habits studies in Maine have shown that woodcock consume a variety of soil invertebrates but depend largely on earthworms, primarily the species *Aporrectodea tuberculata* and *Dendrobaena octaedra* (Reynolds 1977). Because of their highly specialized diet, it seems likely that woodcock use environmental parameters that affect earthworm availability as a means of locating them.

The availability of earthworms at a particular site is a function of both their horizontal and vertical distribution because of limitations on the depth woodcock are able to probe. Vertical distribution is influenced by a species' ecological preferences and by moisture and temperature conditions; horizontal distribution is largely related to soil type (Edwards and Lofty 1977). *A. tuberculata* and *D. octaedra* have been found to occur in soils ranging from gravelly sand to clay, but their highest densities are consistently associated with light loam soils (Guild 1948). Reynolds (1977) reported that these species prefer temperature ranges of 10–18°C and moisture ranges of 15–80%.

The objectives of this study were to determine: (1) whether or not woodcock use physical properties of soil as proximal cues for locating feeding sites, and, if so, which characteristics are important, and (2) the strategies woodcock use to increase their foraging efficiency for earthworms.

Methods

The birds.—The same six adult woodcock were used in all four experiments. Due to injuries to two birds, however, only four were tested in the soil-color and prey-density experiments.

Upon capture, woodcock were wing-clipped and placed in individual holding cages (0.6 × 1.0 × 1.0 m) constructed of 2.5-cm woven-wire mesh with cloth ceilings. The birds were kept indoors under natural light and maintained on an *ad libitum* diet of live earthworms (*Lumbricus terrestris*) and water. Earthworms fed to woodcock in holding cages were covered with moistened sphagnum moss (*Sphagnum* sp.). This was necessary to prevent rapid dehydration. The use of moss also eliminated any potential bias that might have occurred from the use of soil. Woodcock were allowed at least 10 days to adapt to captivity before being used in any experiments.

The testing arena.—Foraging experiments were conducted in a 1.5-m circular arena (Fig. 1) having a 0.5-m woven-wire sidewall, a plywood floor, and an open top. Eight plastic soil trays (23 × 33 × 10 cm) were symmetrically positioned around the perimeter of the arena, recessed flush with the floor, and filled with firmly packed soil. Soil depth in the trays was shallow enough that woodcock could probe to the bottom.

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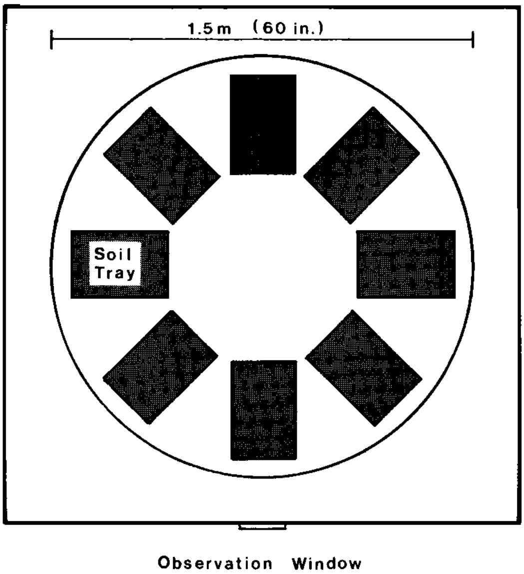

Fig. 1. Design of testing arena used for the feeding trials.

The arena was isolated in a 2.4-m^2 room with sound absorbing walls. This was necessary because extraneous noise and motion tended to interrupt the foraging activity of birds during a trial. Observations were made from outside the room through a 20-cm^2 one-way glass window. To stimulate foraging activity, room lighting was adjusted to approximate the crepuscular periods when woodcock normally feed.

Testing procedures.—Before being used in any experiment, birds were familiarized with the arena and tested for movement patterns. In this test, soil conditions were identical in each tray. One woodcock that did not exhibit a random probing pattern (equivalent probing in each tray) under these conditions was excluded from further testing.

Standardized test procedures were used for all subsequent experiments. Experimental treatments were randomly assigned tray locations within the arena and remained at that location for the duration of an experiment. Each experiment consisted of three replicate trials for each bird on different days. Woodcock were deprived of food for a 12-h period before each trial. To start a trial, birds were released by hand at the center of the arena. During a trial, a bird was allowed to forage for a 10-min period, while an observer recorded its movements, the number of probes, and, when relevant, earthworm captures in each tray. At the end of a trial, the bird was returned to its holding cage and fed.

Experimental conditions.—In the first experiment, woodcock were given a choice of four soil types: sand, sandy loam, loam, and clay loam (Table 1). These represent a wide range of soil textures associated with woodcock habitats in northern Michigan (where this study took place) and were collected from habitats located in the same general geographic area as the birds being tested. Earthworm sampling at the collection sites indicated that all soils except sand were supporting earthworm populations (Table 1). Soils were air-dried to standardize moisture content and screened to remove large debris. Each soil type was then placed in two of the trays in the testing arena. In the second experiment, loam soil was used in all eight trays and moisture content was varied by adding water to each of two trays to achieve 10, 25, or 50% moisture by weight. The remaining two soil trays were left in the air-dried condition. Earthworms were not used in either of these experiments.

To test the role of soil color it was necessary to modify natural soil conditions in order to dissociate color from moisture content and soil texture. This was accomplished by coloring sand with fabric dye. The colors selected for this experiment ranged from light to dark and included a yellow (which closely matched the natural color of sand), a medium green and brown, and black. Water was then added to produce the following color-moisture combinations: yellow, 50%; green and brown, 25%; and black, air-dry. In this way, we held soil texture constant among the trays while creating opposing gradients of color and moisture. This made it possible to separate the effects of color, moisture, and texture. If woodcock cue primarily on texture, we would expect to see equal probing in all the trays, whereas primary reliance on color or moisture would result in concentrated probing activity in the darkest or wettest soils, respectively.

TABLE 1. Classification, texture analysis, and associated earthworm populations of the four soil types used in the experiments.

	Sand	Sandy loam	Loam	Clay loam
Texture analysis[a]				
Percentage of sand	94	58	42	32
Percentage of silt	2	32	36	32
Percentage of clay	4	10	22	36
Earthworm density[b] (number/m^2)	0	78 ± 21	108 ± 32	69 ± 22

[a] Based on hydrometric determination (Foth and Turk 1972).
[b] Samples taken at site where soils were collected using a formalin extraction technique (Reynolds et al. 1977).

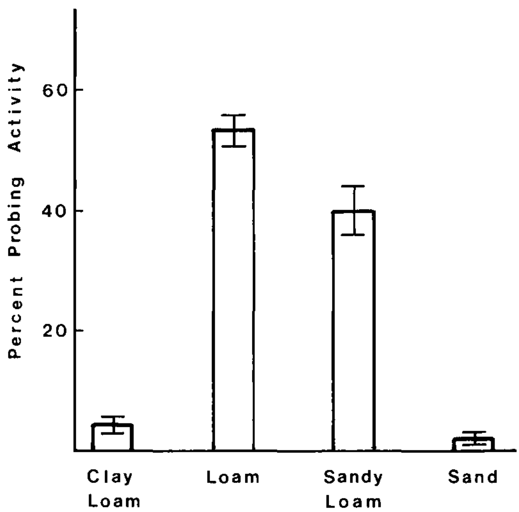

Fig. 2. The average (±SE) percentage of probing activity by six woodcock among the four soil types tested.

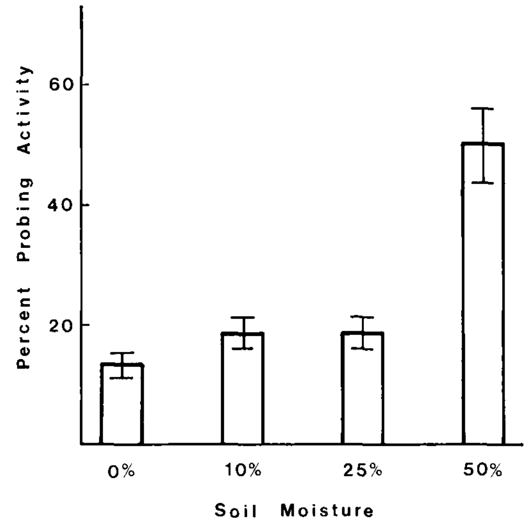

Fig. 3. The average (±SE) percentage of probing activity by six woodcock in loam soils of varying moisture content.

To test woodcock foraging efficiency in relation to prey density, we used loam soil with 40% moisture in all the trays. Live *L. terrestris* were used as prey and were randomly placed 2–6 cm below the soil surface just before each trial. All earthworms were equivalent in size. Each of two trays was assigned either 0, 2, 4, or 8 earthworms.

Analysis.—Data in this paper are presented as percentages of total probing activity during a trial. We performed the statistical analysis, however, on the actual number of probes per tray and used a two-factor mixed-model analysis of variance (ANOVA), in which experimental treatments (moisture, texture, color, or prey density) and individual birds were considered main effects. The first-order interaction was used to evaluate the consistency of treatment response between individual birds. Data were transformed with $\log_{10}(\bar{x} + 1.0)$ to improve among-group heterogeneity. Tukey's HSD test (Gill 1978) was used to make all pair-wise comparisons of treatment means. In all cases, statistical significance was set at the 0.05 probability level.

Results

Woodcock exhibited pronounced preferences among the four soil types tested (F = 81.49; df = 3,15; $P < 0.001$), with loam and sandy loam receiving 94% of all probing activity (Fig. 2). Pair-wise comparisons of individual treatment means showed that probing activity was significantly different between each of the soil types except sand and clay loam. Examination of the treatment-bird interaction term (F = 1.69; df = 15,120; $0.10 > P > 0.05$) suggests that there was some individual variability in the degree of preference for the four soil types. Individually, however, all six birds did far more probing in loam and sandy loam soils than in sand and clay loam. These results show that woodcock do discriminate between soil types, but it is not clear which physical characteristic of the soil they are cuing on. There were obvious differences in texture between the soils tested, but there were also noticeable color differences; the sand and clay loam were much lighter in color than the loam and sandy loam.

There were some striking similarities between the relative amount of woodcock probing activity in the laboratory and corresponding earthworm densities at the soil collection sites (Table 1). Of the four soil types, loam was most preferred by the birds, and it supported the greatest earthworm density. Likewise, birds spent the least effort (5%) probing in sand, which supported no earthworms. The differences in probing activity between clay loam and sandy loam, however, were much greater than the corresponding observed earthworm densities.

In response to soil-moisture content, woodcock again showed significant overall prefer-

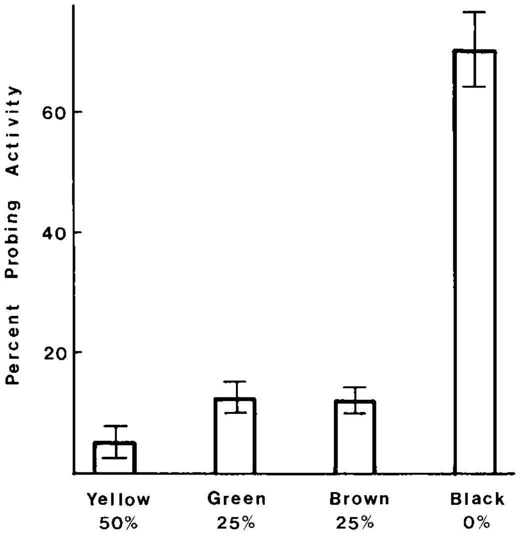

Fig. 4. The average (±SE) percentage of probing activity by four woodcock in color-dyed sandy soil with varying moisture content.

ences ($F = 13.67$; df = 3,15; $P < 0.001$), with 51% of all probing taking place in the wettest soil trays (Fig. 3). Although differences between the three drier soils are not statistically significant, there is a trend of increased probing activity with increasing moisture content. In this experiment, the treatment-bird interaction showed that all six birds exhibited equivalent patterns of preference ($F = 1.20$; df = 15,120; $P > 0.25$). These results suggest that the birds are able to detect differences in soil-moisture conditions. This interpretation, however, is confounded by the fact that soils become darker in appearance as moisture content increases.

When the same birds were tested using color-dyed sand, they exhibited significant preferences ($F = 60.50$; df = 3,15; $P < 0.001$) for the darkest soil conditions. Of all probing activity, 70% occurred in the air-dry black soil, while only 4% took place in the yellow soil with 50% moisture (Fig. 4). Nearly equal amounts of probing took place in the green and brown soils. As in the first two experiments, all six birds showed equivalent patterns of preference ($F = 0.57$; df = 9,80; $P > 0.50$) among the various color-moisture combinations. The nearly equal probing activity in the green and brown soils suggests that woodcock depend more on color value (the brilliance of a color, Foth and Turk 1972: 59) than hue (color wavelength) as a basis for discriminating soil conditions. This is probably related to the fact that woodcock eyes are adapted to conditions of dim light and have a higher rod-to-cone ratio than diurnally active birds (Dyer 1976).

Significant differences in probing activity also occurred relative to variations in prey density ($F = 10.39$; df = 3,9; $P < 0.01$), with the greatest amount of probing in trays containing the largest number of earthworms (Table 2). A pairwise comparison of treatment means showed that significantly less probing took place in trays containing no prey, significantly more occurred in trays with 8 prey, and there was no difference between trays containing 2 and 4 earthworms. As reflected by the similarity of capture-efficiency data, numbers of prey captured in a tray during a trial were approximately proportional to the initial prey density. The number of probes per capture declined significantly, however, as the number of earthworms in a tray increased. On the average, woodcock caught 48% of the available prey in each tray during a trial. Again, individual birds exhibited equivalent patterns of selectivity ($F = 0.25$; df = 9,80; $P > 0.50$).

During this experiment, we observed woodcock using two distinct types of probing while foraging: exploratory and pursuit. Exploratory probes were used only to detect the presence of earthworms, while pursuit probes were used

TABLE 2. Summary of probing activity and capture success ($\bar{x} \pm$ SE) of four woodcock in response to various densities of equal-sized prey.

	Prey density			
	0	2	4	8
Percentage probing activity	17 ± 1	25 ± 1	24 ± 2	37 ± 1
Total captures	0	7	12	17
Capture efficiency[a]		45 ± 11	43 ± 12	56 ± 21
Number probes/capture		22 ± 3	12 ± 2	9 ± 3

[a] Capture efficiency is the percentage of prey caught out of the total number available.

to capture prey. Exploratory probes were characteristically shallow (less than half the bill length), and birds paused momentarily following insertion of the bill into the soil. Exploratory probes were generally several cm apart. In contrast, pursuit probes were deeper (often the full length of the bill), occurred in rapid succession, and were concentrated in a very small area.

Woodcock foraged by probing from side to side as they walked through an area (in the experimental arena this tended to be a circular path around the perimeter). When an earthworm was detected with an exploratory probe, birds quickly followed with one or more pursuit probes. If unsuccessful in capturing an earthworm, birds simply continued moving along their original search path. When successful, however, they nearly always concentrated further exploratory probing in the same general area as the previous capture. Only after extensive searching without additional success did birds once again begin searching in new areas.

Discussion

The results of these experiments show that woodcock employ specific strategies both for locating good feeding sites and for increasing their efficiency at capturing earthworms. When selecting feeding sites, woodcock use soil color as an indicator of site quality, even though it has no direct affect on earthworm densities. In so doing, the birds apparently depend on the fact that soil color correlates with the soil conditions (soil types and moisture) that directly influence earthworm abundance. Organic matter content is known to be an important determining factor of soil color (Foth and Turk 1972) and is also an important food source for earthworms (Edwards and Lofty 1977). Soils associated with woodcock habitat in northern Michigan are predominately sand to sandy loam types (Veatch and Schoenmann 1924). Consequently, in this part of the bird's range, darker soils generally contain greater amounts of organic matter and support higher densities of earthworms.

There is evidence to suggest that under certain conditions the strong reliance on color as an indicator of site quality may cause birds to overlook potentially good sites. This appears to be the case in the first experiment (testing four soil types) where woodcock probed very little in the lighter-colored clay loam soil. Field sampling for earthworms indicated that densities in this soil type were nearly equal to those in the darker sandy loam soil, where birds did concentrate searching effort.

Likewise, color may also lead woodcock to forage in unproductive areas. Birds have been observed (Rabe unpubl. obs.) probing in dark mud-puddle basins along sandy trail roads and were apparently misled by the thin layer of dark silt accumulation. Sampling showed that no earthworms existed at these sites.

It is also possible that the use of color could stimulate birds to select feeding sites with suboptimal moisture conditions for earthworms. Assuming that soil continues to darken as moisture levels approach saturation, then levels beyond the preferred range (>80%) for earthworms would appear very dark and be perceived as good feeding sites. We suspect, however, that birds rarely encounter this problem, because the coarse-textured soils in our study area drain rapidly and generally are saturated for only a short period during the spring. Also, it has been shown that earthworms are much more tolerant of saturated soils than of dry soil conditions (Edwards and Lofty 1977).

Even though there are potential shortcomings from using color as a proximal cue, there are several advantages as well. First, it means that birds need monitor only one soil characteristic to improve their chances of selecting good feeding sites. Otherwise, it would be necessary for birds to monitor at least two soil parameters (soil type and moisture) in order to assess site quality and seasonal variation in earthworm availability. Second, woodcock can visually evaluate soil coloration more rapidly than perform the extensive probing required for direct monitoring of soil conditions. It is even conceivable that woodcock using color could make cursory site evaluations from the air.

Relative preferences of soil types during the first two experiments lead us to believe that birds use soil color to evaluate habitat quality at different levels. In the first experiment, when birds chose between four different soil types, the majority of probing (57%, Fig. 2) was in the air-dry loam soil. In the second experiment, when all trays contained loam soil, the least amount of probing (only 13%, Fig. 3) was in the air-dry trays. The immediate and dramatic shift in preference for the same soil conditions indicates that birds are continually making comparative evaluations of foraging sites and are not using a fixed "color-search-image." It seems likely, then, that birds use color to make gross comparisons of soil types between various habitats, and again on a much finer scale to select the best soil moisture conditions within a soil type.

In the last experiment, woodcock concentrated their searching effort in areas of relatively high prey density. There is no evidence to suggest, however, that birds are able to evaluate prey density from their exploratory probing. Rather, the concentration of searching effort seems to be a function of the nonrandom foraging pattern used following an initial prey capture. This type of strategy is adaptive when prey occur in aggregated groups or are at very high densities, because woodcock can use locational information from one capture to improve their chances of finding additional prey. On the other hand, if prey are randomly distributed, this type of strategy would actually be less productive than completely random probing. Edwards and Lofty (1977) and Satchell (1955) found that earthworm reproduction, as well as local variations in moisture and food supply, frequently result in aggregations of earthworms even within relatively homogeneous soil types. It appears, therefore, that woodcock have evolved the nonrandom foraging strategy in response to a nonrandom distribution of its primary prey.

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